Growth of a jumping spider on nitrogen enriched prey

Toshinori Okuyama

Department of Zoology, University of Florida, Gainesville, FL 32611−8525
E-mail: okuyama@rice.edu

Abstract — The jumping spider, *Phidippus audax* (Hentz), preys on other spiders both intra- (cannibalism) and inter-specifically (intraguild predation). Smaller individuals become the victims in these predations. One hypothesis for the evolution of IGP/cannibalism is that consuming other carnivores (e.g., spiders) decreases a dietary stoichiometric imbalance because carnivorous prey have higher nitrogen contents than herbivorous prey. This study examined whether the nitrogen content of prey affects growth patterns of spiders by using fruit flies whose nitrogen contents were artificially enhanced. Spiders that were raised on the nitrogen rich prey grew faster than those raised on unmanipulated prey, by shortening moulting intervals. This result is consistent with the stoichiometric argument and would also have important consequences to the community dynamics of these organisms, by altering the size structure of communities with IGP and cannibalism.

Key words — intraguild predation; cannibalism; stoichiometry; nitrogen limitation; jumping spiders

Introduction

Nutrient contents of food resources have important influences on consumer behavior, fitness and population dynamics. For example, nitrogen levels of plants influence demographic parameters (i.e., growth and fecundity) of grasshoppers (Joern & Behmer 1997). Feeding activities and growth rates of zooplankton are strongly influenced by phosphorus levels in their algal diet (Plath & Boersma 2001). Theoretical models of foraging behaviors suggest that animals should forage selectively to maximize their nutrient requirements (e.g., Simpson et al. 2004). These considerations are important not only for understanding behavioral and physiological mechanisms of foraging but also for understanding dynamics of ecological communities because nutritional details directly affect the functional and numerical responses of species interactions (Andersen et al. 2004). In recent years, analysis of community models with nutrient specific interactions has become common (e.g., usually called ecological stoichiometry (Loladze et al. 2004) or nutrient homeostasis (Logan et al. 2004)) and these studies have helped to describe previously unexplained patterns in nature (reviewed in Moe et al. 2005).

Intraguild predation (IGP), predation among individuals of the same guild, has been suggested to be a response of predators to the mismatch in the ratio of carbon to nitrogen (C: N) between predators and herbivorous prey (Denno & Fagan 2003). The ratio of C: N decreases as trophic level increases (Fagan et al. 2002). IGP benefits the predators (i.e., intraguild predators) because consuming other nitrogen-rich organisms (carnivorous prey) helps to satisfy their nutrient requirements and would facilitate growth processes (Fagan & Denno 2004).

As a direct examination for the stoichiometric hypothesis, Matsumura et al. (2004) examined the effect of prey type on the growth of the wolf spider *Pardosa littoralis*. On the contrary to the hypothesis, spiders on a carnivore diet did not grow better than spiders on a herbivore diet. However, because different prey items would also vary in aspects other than their nitrogen contents, to what degree the nitrogen content was responsible for the growth of the predators is difficult to infer.

Jumping spiders are generalist predators that exhibit IGP. Because of frequent and size-dependent IGP (Okuyama 2007), jumping spiders are ideal subjects for studying the relationship between prey quality and the development of predators. If IGP facilitates the growth of intraguild predators, it would directly affect the size-structure of the community, which in turn affects the interactions of IGP because the occurrence of IGP is size-dependent (Polis 1988). In this study, I examined whether the nitrogen content of prey affects the growth of the jumping spider, *Phidippus audax*, by using prey whose nitrogen contents were artificially manipulated.

Materials and methods

Eggs of the jumping spider *Phidippus audax* (Hentz) were collected in a field near the campus of the University of Florida, Gainesville, FL, USA. First instar spiderlings do not eat before becoming second instar spiderlings. Once the spiders moulted to the second instar, they were assigned to one of the two treatment groups: control and nitrogen-rich (N-rich). The spiders were individually reared in plastic cups (62 mm in diameter and 30 mm in height; approximately cylindrical). Forty spiders were used in each treatment. Mean ($\pm$ sd) carapace width of the spiders in the

beginning of the experiment was 0.83 ± 0.05 mm (N-rich) and 0.84 ± 0.04 mm (control); they were not statistically different (Welch two sample t-test, $t_{75.21} = 1.408$, $p = 0.1633$).

Experimental treatment

Spiders in the two treatment groups received prey (*Drosophila melanogaster*) that were reared on different media to alter their nutrient profiles (Mayntz & Toft 2001). In control group, fruit flies were raised on *Drosophila* medium obtained from Carolina Biological Supply Company (Burlington, NC, USA). In N-rich group, blood meal (Pennington Seed, Madison, GA, USA) was added to the medium (3:1 = medium: blood meal). Nutrient contents of the flies from the two treatments were measured with Carlo Erba NA1500 CNS elemental analyzer. One sample ran with five individuals, and two samples were used for each prey type, which was sufficient to confirm the effectiveness of the treatment; nitrogen contents (%N) of the flies were higher in N-rich group. The nutrient contents of spiders were also examined to verify the accumulating evidence about the higher nitrogen content for predators (Fagan & Denno 2004) also holds in the study system.

In order to examine potential confounding factors of the treatment (i.e., treatment may create differences in aspects of prey in addition to the nitrogen content), energetic contents of prey were also quantified based on a whole-animal assay with a dichromate oxidation method described in McEdward & Carson (1987). Five individuals were used for each prey type as the replication.

Effect on growth

Spiders were kept in a controlled environmental chamber (28°C, light: dark = 14:10 h). One fruit fly was given every three days during the second instar. Two fruit flies were given every three days during the third instar and the fourth instar. The spiders were able to consume all the prey provided to them within a day although the prey were given only once every three days. This procedure made sure that results were not confounded by the differential amount of prey consumption. For example, if spiders in N-rich group consumed more flies than ones in control, it is difficult to tease apart the effect of nitrogen. Water was supplied daily with a water-soaked sponge. Carapace widths of spiders were recorded within 24 h of their moulting events to examine the treatment effect on the size. The durations of each instar were also recorded to examine the effect on growth rates. These indices (i.e., instar duration and carapace width) were chosen rather than weight (Matsumura et al. 2004) because jumping spiders' weights fluctuate simply by their water consumption, and thus the indices were thought to be more reliable reflections of their development.

One spider in N-rich group died during the experiment and was excluded from the study. Thus, for all the following analyses, the sample size for control group was 40 while the sample size for N-rich group was 39. Treatment effects on growth (size and instar duration) were analyzed with

Welch two sample t-test.

Results

The fruit flies that were raised on blood meal were significantly higher in their nitrogen content than ones in control (Welch two sample t-test: $t_{1.183} = 9.2783$, $p = 0.048$), but their energetic content was not statistically different ($t_{7.389} = -0.81$, $p = 0.445$). The spiderlings consisted of high nitrogen contents (Table 1) and the nitrogen content of the spiderings and that of N-rich flies were equivalent ($t_{1.456} = 0.4724$, $p = 0.70$).

Individuals in N-rich group had wider carapaces on average for all the instars examined, but the differences of carapace growth were not statistically significant (Fig. 1; Welch two sample t-test: [second instar] $t_{64.56} = 0.624$, $p = 0.53$; [third instar] $t_{76.84} = 0.769$, $p = 0.44$, [forth instar] $t_{64.29} = 0.239$, $p = 0.81$). The size difference was insignificant even when the cumulative difference was considered (i.e., the changes in size from the second instar to the fifth instar).

Mean instar durations were always shorter for N-rich group (Fig. 2). These differences were statistically significant for the second instar and the forth instar (Welch two sample t-test: [second instar] $t_{73.24} = 3.57$, $p = 0.0006$; [forth

Table 1. Nutrient and energy contents of prey (standard errors in parentheses).

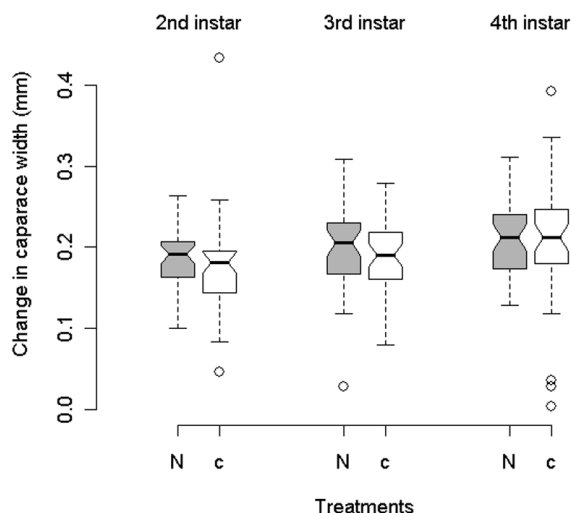| Prey	%N	%C	Energy (J)
flies: contol	7.64 (0.08)	50.38 (0.26)	2.20 (0.48)
flies: N-rich	10.36 (0.28)	49.59 (0.94)	1.71 (0.36)
spiderlings	10.06 (0.57)	35.88 (1.27)	1.50 (0.26)

Fig. 1. Growth in the carapace width of spiders. *n*th instar data indicate the difference in size between $(n+1)$ th and *n*th instars. No significant differences were found between the treatment groups. Treatment: N-rich (N) and control (c). Top and bottom lines of the box indicate the 75% quartile and 25% quartile of sample, respectively. The horizontal bar in the box indicates the median. Top and bottom bars around the box indicate 90% quartile and 10% quartile, respectively. The upper and lower notches correspond to the upper and lower 95% CI about the median. Circles are data points identified as outliers.
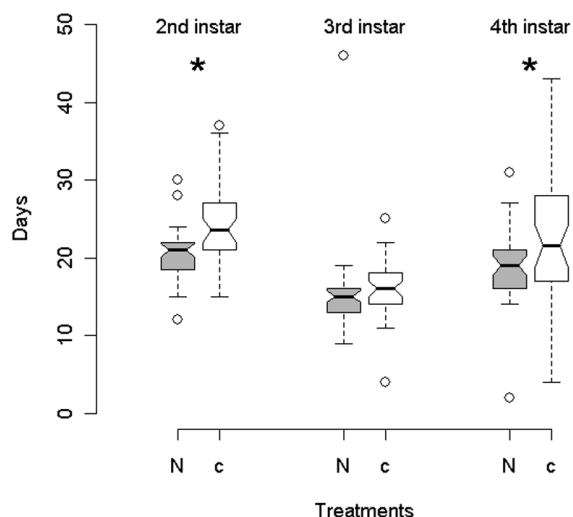
Fig. 2. Duration of each instar. Durations of 2nd instar and 4th instar were significantly smaller for N-rich group (indicated by*). Treatment: N-rich (N) and control (c).

instar] $t_{63.75} = -3.09$; $p = 0.003$), but not significant for the third instar ($t_{63.88} = 0.204$, $p = 0.839$).

Discussion

Consumption of the nitrogen enriched prey facilitated the growth of jumping spiders through shortened moulting intervals. Although there was no statistically significant difference in carapace width, the effect on moulting durations would strongly affect species interactions. This is because IGP is size-dependent; individuals that moult faster and thus become larger faster would have a selective advantage when IGP is frequent as in these jumping spiders (Okuyama 2007).

Future works may benefit by considering prey's nutrient profile in detail. Matsumura et al. (2004) documented that a carnivore diet did not facilitate growth of the wolf spider *Pardosa littorais*. However, when the predators were raised on a mixed diet (predators and herbivores), the mixed diet increased the performance. Researchers have found similar results (i.e., advantages of mixed diets) in other ecological systems (Agrawal et al. 1999; Cruz-Rivera & Hay 2000). We still do not clearly understand the optimal nutrient requirements for these carnivores, nor how those nutrients are distributed among prey in the field. Nor do we know whether simplifying the description of stoichiometry to a single C: N ratio (or C: N: P) is adequate for understanding community dynamics. For example, Greenstone (1979) found that wolf spiders forage selectively to optimize amino acid makeup, which suggests that more complex nutrient descriptions may be necessary for studying the role of nutrient balance in community ecology.

In this experiment, the diet of prey (i.e., fruit fly medium) was manipulated to vary the nitrogen content of the prey (Mayntz & Toft 2001). It is not certain whether the level of nitrogen difference between the treatment groups was created as a result of nitrogen assimilation into fly tissues or blood meal in their gut content. This difference is not crucial to some interpretation of this study because the spiders that developed faster nonetheless consumed the prey that were rich in nitrogen but were not richer in the energetic content. However, the results have other implications. For example, nitrogen content varies greatly among plants (Mattson 1980). Anthropogenic environmental changes (e.g., increased CO_2 and soil pollution) alter nutrient levels of plants (Newman et al. 2003). The blood meal used in this study is a common agricultural fertilizer. If herbivores that consume plants of different qualities influence predators as shown in this study, the effect of stoichiometric interaction on systems with IGP could occur at very large temporal and spatial scales. By carefully examining nutrient requirements of organisms as well as the flows of nutrients, we may obtain deeper insights not only into a specific ecological community with IGP but also into the general properties of the persistence of complex food webs.

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